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# The Winter Feeding of the Oystercatcher (*Haematopus ostralegus*) on the Edible Mussel (*Mytilus edulis*) in the Conway Estuary, North Wales

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# CONTENTS


INTRODUCTION . . . . . *Page* 1

OBSERVATIONS . . . . . 1

Behaviour of the Birds . . . . . 2
Daily Routine . . . . . 2
Morfa . . . . . 2
Pensarn . . . . . 2

Feeding Behaviour . . . . . 2
Morfa . . . . . 3
Pensarn . . . . . 3

Damage to Opened Shells . . . . . 4
Pensarn . . . . . 4
Morfa . . . . . 4
Relation to Shell Form . . . . . 5

Food Intake . . . . . 7
Morfa . . . . . 7
Pensarn . . . . . 9

Food . . . . . 10

Bird Numbers . . . . . 13

Predation . . . . . 13

DISCUSSION . . . . . 14

SUMMARY . . . . . 15

REFERENCES . . . . . 15

# The Winter Feeding of the Oystercatcher (*Haematopus ostralegus*) on the Edible Mussel (*Mytilus edulis*) in the Conway Estuary, North Wales.

## INTRODUCTION

THE main diet of the oystercatcher on the sea coast is molluscan and for this reason the bird is generally believed to be the arch enemy of shellfish exploitation. Lambert (1951) cites the birds as 'les redoubtable enemis des moules'. The importance of oystercatcher predation in the economy of a cockle bed has already been investigated (Drinnan, 1957); the present study was designed to provide information, which, with the minimum of local observation, would allow an estimate to be made of oystercatcher predation on any mussel-bearing area.

The area studied was the estuary of the Conway River in North Wales. Here a thriving mussel-fishing industry is centred on the extensive mussel beds at the mouth of the river, which also provide a winter feeding ground for some hundreds of oystercatchers.

The majority of the observations were made on the main beds but a brief study was made on a discrete flock of birds which fed on the steep, mussel-covered banks immediately above Conway bridge, where the close proximity of the birds to a laboratory on the shore made prolonged observation convenient. Below, these areas will be referred to as the Morfa (mussel beds) and Pensarn (above the bridge). Observations made in the two areas will be described together except where they differ.

Dewar (1908, 1913, 1915) studied oystercatcher feeding in the Firth of Forth with special reference to the chief source of food in that area, the mussel. Very little quantitative information is available from this work, though a comparison with our results shows some interesting differences.

The Morfa mussel beds are extensive, covering both banks at the mouth of the river, alongside the channel. Mussels occur from a level of $2\frac{1}{2}$-3 hours ebb down to below low water mark.

At Pensarn, above the bridge, a small flock, constant in number throughout the winter, feeds on the mussel-covered shores. The distribution of mussels with tidal level is much the same here as on the beds at the mouth of the river.

## OBSERVATIONS

OBSERVATIONS were made during the winters of 1954/55 and 1955/56. Special attention was given to the problem during the latter winter, but where comparable observations were made in 1954/55 these agree with later results. From August 1955 to March 1956 the writer was resident in the district and both areas were visited at least once a week, in order to make observations on feeding. Additional visits were made to the beds for other purposes, on all of which details of bird numbers, distribution and behaviour were noted.

On the Morfa, observations were usually made from the sandhills above high water mark, at a range of ca. 200 yards from the uppermost mussels. Binoculars ($7 \times 50$) were used for general observation and a telescope ($\times 60$) for more detailed work. At Pensarn observations were normally made from the laboratory on the foreshore within 200–250 yards of all the feeding grounds.

## BEHAVIOUR OF THE BIRDS

The summer population of oystercatchers in the Conway estuary is less than fifty birds. The winter flocks, studied in this work, are present from the beginning of August to the end of March. Both ringing returns and the date of arrival of the birds suggest that they are British breeding birds. They arrive well in advance of the birds studied on the Lancashire coast which were thought to be migrants from northern breeding areas (Drinnan, 1957).

### DAILY ROUTINE

The birds show a cycle of activity correlated with the rise and fall of the tides, feeding where mussels are uncovered until the rising tide forces them off. High tide periods are spent in roosting flocks along the shore line.

The tidal cycle of feeding has been described before (Dewar, 1915, Drinnan, 1956); Dewar also mentions a fortnightly rhythm of behaviour, an anticipation of the increased height of the spring tides, in the formation of the roosting flocks. Both in the present survey and during earlier work (Drinnan, 1957) there was no indication of such a rhythm, the birds always forming flocks as low down on the beach as possible, and only moving up when forced to do so by the rising tide.

It has been noted (Dewar, 1915, Drinnan, 1957) that the tidal cycle of feeding continues in the hours of darkness. This was also found in the Conway estuary. On moonlit nights birds could be seen feeding and on three occasions in the winter of 1955/56 the beds were visited at first light after a night with no moon. On each of these visits a low tide period had occurred in which mussels were exposed only during darkness. On each occasion a litter of freshly-opened shells was found at a concentration seemingly no different from that found in daylight feeding. No more exact information on night feeding is available.

### MORFA

Mussels of all sizes are available in this area, but at the time of the observations large areas of the beds, especially at the higher levels, were covered by a dense carpet of young mussels 10–35 mm. in length. The distribution of birds feeding on the beds was not uniform. Feeding was concentrated on the areas containing these small mussels and this concentration of feeding birds persisted throughout the low tide period, even on the higher levels.

Two flocks of roosting birds were formed at high water, one below Morfa Point and the other at the head of the bay below Penmaenbach. The flock at Morfa Point persisted through a neap high tide but on a spring tide these birds joined the flock below Penmaenbach an hour or so before high water. The two flocks were relatively constant in numbers throughout the winter and appeared to be distinct units.

### PENSARN

Here mussels of all sizes were available on the shore in a mixed population. The distribution of the birds was uniform over the mussel-bearing areas, feeding taking place at all levels, even at the time of low water. The area is divided into three feeding grounds by the channels of the Conway river and Gyffin stream. The birds usually fed as a flock on one of these areas, selecting that most remote, for the time being, from human activities.

The high water roost for these birds was below Conway Castle, on the left bank of the river, on a strip of grass, covered only on extreme high water spring tides.

## FEEDING BEHAVIOUR

In the two areas the birds were feeding on very different sizes of mussels. As this influenced their feeding behaviour the areas are treated separately below.

## MORFA

The small mussels on which the birds fed were lying on gravel or muddy sand, with occasional stones. The mussel cover was dense, but clear areas of sand, muddy gravel or large stones occurred between patches of mussels. The size range of opened mussels found here was 20–35 mm.

Feeding birds walk forward over the beds with head bowed and beak pointing downwards. Exploratory probes are made, many of which are not followed by an attempt at opening. Although some mussels were seen to be opened *in situ*, the majority were separated from the substrate before opening.

The mussel is either seized and torn from its position or dislocated by a jab or two from the bill. It is then picked up by either the byssus, or the shell, and carried to the place where it is to be opened; this may be several yards away. A series of vigorous jabs is then made with the bill closed, six or eight usually being sufficient to allow penetration of the shells. The mussel may be re-positioned between jabs, though it is seldom moved to a new place. During the jabs the angle of attack is often altered as though to follow a particular region of the shell as it moves. When the beak enters the shell the mandibles are separated, the meat grasped and the shell separated by vigorous shaking. The meat is swallowed and the shell is often cleaned by a snipping action of the tips of the bill. Opening seldom takes as long as one minute and is frequently performed in 10–15 seconds.

Where the birds were feeding, the sand surrounding the patches of mussels was often littered with opened shells and birds often carried mussels many yards to such sandy areas. Other favoured areas for opening were the tops and sides of stones on the mussel beds, though many shells were opened on the apparently homogeneous surface of the mussel beds. Several times a bird was seen to carry a series of shells to the same spot for opening. One bird was seen to open eight mussels in succession on the top of a flat stone, where eighteen newly opened shells were subsequently found.

Dewar (1908) describes the carrying of mussels to rocks for opening and also (1913) concentrations of shells of *Mytilus* and other food animals.

The birds showed no dependence on mussels newly uncovered by the tide, as suggested by Dewar, nor was there any suggestion that opening was any easier under such conditions. At the beginning of the tidal period the birds fed in shallow water and then moved down with the tide to the lower reaches of the beds, but their rate of feeding did not differ from that of birds at higher levels, on mussels which had been dry for some hours. On a patch of small mussels at the upper limit of the beds, birds fed throughout the tidal cycle at a constant rate, the same as that of birds at all other levels.

Birds often fed in shallow water, at the edge of the tide or in pools on the beach. Feeding here was as on the dry ground, mussels being carried to dry ground for opening.

## PENSARN

The mussel population is a mixed one of all sizes. Those eaten by the birds ranged from 20–60 mm. The mussels are distributed patchily over the shelving beaches from a height of 2–3 hours ebb down to a sub-littoral level, the substrate ranging from soft mud, with occasional stones, through sand and stones to rock.

The close proximity of the birds enabled very detailed observation of feeding to be made. Attacked mussels were separated from other mussels, or stones to which the byssus was attached, and then carried to the place where they were opened. Only once was a bird observed to open a mussel without removing it from the bed.

Opening was effected on patches of sand or stones, or rock. The shell was placed ventral side upwards before attack and frequently re-orientated to this position. The ventral fissure of the shell was the usual target for a series of very vigorous blows with the closed beak, though rarely the posterior border of the shell was attacked.

Small mussels of the size opened on the Morfa (up to 30 mm.) were dealt with as described earlier. Larger mussels were opened in the following manner. When the bill entered the shell, usually by the breaking inward of a semi-circular portion of the ventral

shell border, the bill was directed to the posterior of the shell where a jab or two severed the posterior adductor muscle. The valves were now separated by a forceps action of the bill and the anterior regions of the shell, towards the umbo, were attacked in a series of thrusts. The meat, now freed from its major attachments, was seized, shaken free and swallowed. A scissors-like action of the mandible tips completed the cleaning of the shell, leaving only shreds of the adductor muscles. Our observations suggest that the mussel is usually placed with its anterior end towards the bird, *ca.* 75% of the mussels observed being initially orientated in this way. No matter what the initial orientation the anterior adductor muscle is always attacked from this position, the bird moving round the mussel after having gained access to the shell.

A few mussels were seen to be opened through the posterior border, the procedure being similar to that described above. Access to the shell usually resulted in severance of the posterior adductor muscle. Shells opened in this way were placed with their posterior end to the bird. The only mussel seen to be opened *in situ* was orientated this way.

In the areas studied, the nature of the bottom, mostly sand and stones, appeared to have little effect on the speed of opening of mussels. However, on the opposite side of the river to the Morfa feeding-ground, there was a large bed of mussels, similar in size to those eaten at Morfa, but lying on soft mud. It was observed that the birds never fed on this bed. It seems that mud does not offer sufficient resistance to permit the opening of mussels. The frequent carrying of mussels, in the feeding area, to a firm substrate, stones or sand, for opening, supports this.

## DAMAGE TO OPENED SHELLS

### PENSARN

Here opened shells were found either lying on the dorsal surface with valves gaping widely and the dorsal regions of the shell embedded in the substratum, or with the anterior of the shell embedded. The shells usually showed jagged semi-circular pieces broken from the ventral region. Often there were cracks running from these holes to the dorsal or posterior borders of the valves. Of 350 shells collected at random from the three feeding grounds at intervals throughout the winter, 74% showed this damage to the ventral border, 4% similar damage to the posterior border, 1% to the dorsal border and 21% showed no damage at all. These observations agree very well with the observed behaviour of the birds.

In the sample of opened shells referred to above, only 2% showed damage to both valves. Damage to the left valve was found in 32%, damage to the right valve in 45%, while 21% showed no damage at all.

### MORFA

Here detailed observation of the method of opening shells was impossible. Opened shells were usually found lying either on the dorsal edge or on the undamaged valve. The concentration of such shells, on areas favoured for opening, often resulted in opened shells being trodden into the bottom or otherwise disturbed by the birds. Damage to the valves was more extensive than at Pensarn, the damaged valve often being represented by no more than a strip adjoining the ligament. For this reason, in all the shells used for the analysis below, all the fragments of the broken valve were collected and the valve reconstructed. From 500 such shells collected during December 1955 and January 1956, the following information was obtained. A conclusion as to the point of attack was, as at Pensarn, drawn from the presence of small V-shaped chips in the shell margin. In these smaller shells, chips were usually accompanied by splits radiating from them and producing the much reduced valve described above. Of the sample 83·5% showed attack to the ventral margin, 3% to the dorsal margin, 1·5% to the posterior margin and 12% showed no damage. As at Pensarn, damage was usually restricted to one valve; only one shell in the sample showed

damage to both valves; of the others, 36% had the right valve damaged and 52% the left.

In both areas damage to only one valve was general. This had been described before in feeding on *Mytilus* (Dewar, 1908, 1913), *Modiola* and *Tapes* (Dewar, 1913), and *Cardium* (Drinnan, 1957). Dewar (1913) considering the opening of *Mytilus*, suggests that a displacement of one valve relative to the other occurs, caused by the first blows of the bill, before the adductor has been severed, damage by subsequent blows being confined to the overlapping valve. Such a rotation is easily accomplished in closed mussels but could not be observed in the field.

## RELATION TO SHELL FORM

It was shown (Drinnan, 1957) that oystercatchers, when feeding on cockles, gained access to the shell at its most vulnerable point, and the suggestion was made that this is the result of a random application of effort. In the case of the mussel the same correlation can be shown between damage to opened shells and shell structure; the feeding behaviour of the birds is closely adapted to the problem of opening mussel shells.

The resistance to attack of the margins of the valves of a closed shell will depend on four factors:

(1) The thickness of the valve margins;
(2) The size of the angle between them;
(3) The degree of apposition between the margins;
(4) The force causing this apposition.

From the analysis of the opened shells it is seen that the strength of the shell margin depending on (1), (2) and (3) is the limiting factor in most cases. Only 12% (Morfa) and 21% (Pensarn) of the opened shells show no damage to the shell. In these presumably the force exerted by the adductor muscles was overcome by an effort less than that required to break the shell. Many or all of these may have been attacked when the shells were open, under water. But the possibility of the failure of the adductor muscles, after damage to the valve margin, to allow leverage by the bill merits a consideration of the regional variation in the force required to overcome the tension of the adductor muscles.

If the shell valve with its adductor muscles, of which the posterior is the largest and most important, is considered as a lever pivoting on the plane of the hinge then it is apparent that the force required to overcome the adductor muscles decreases progressively along the dorsal and ventral margins, reaching a minimum at the border between posterior and ventral margins.

The mechanical resistance of the valve margins to blows will depend on their own strength and on the support they lend to one another. In the mussel the innermost, nacreous, layer is secreted by the whole of the mantle surface and so the thickness of the shell at any given distance from the umbo increases with age. The shell becomes progressively thinner as one progresses from umbo to shell margin. The thickness of the shell margin shows no appreciable regional variation but the rate of increase in thickness of the valve with distance from the margin varies substantially, being greatest ventrally, less dorsally and least posteriorly (Fig. 1). The size of the angle between the valves governs not only their degree of support for one another, but also their resistance to shear when acted upon by a force in the plane of their margins. The angle the valves make with the median plane of the animal is least posteriorly, slightly greater dorsally and much greater ventrally. The support the valves lend to one another decreases with the size of this angle but also depends on the degree of apposition of the valves. When the mussel is closed the valves seal well, the shells retaining water, but at the ventral margin, where the byssus emerges from the shell, the seal is maintained only by the flexible and relatively thin outer layer of the shell, the periostracum. The shell valves proper do not meet here.

Greatest resistance to entry will come from good muscular adduction, a thick shell margin, a small angle between valves and close apposition of the valves.

Summarising: at the dorsal margin the muscular adduction is great, the shell intermediate in thickness between ventral and posterior margins, the angle between shell valves

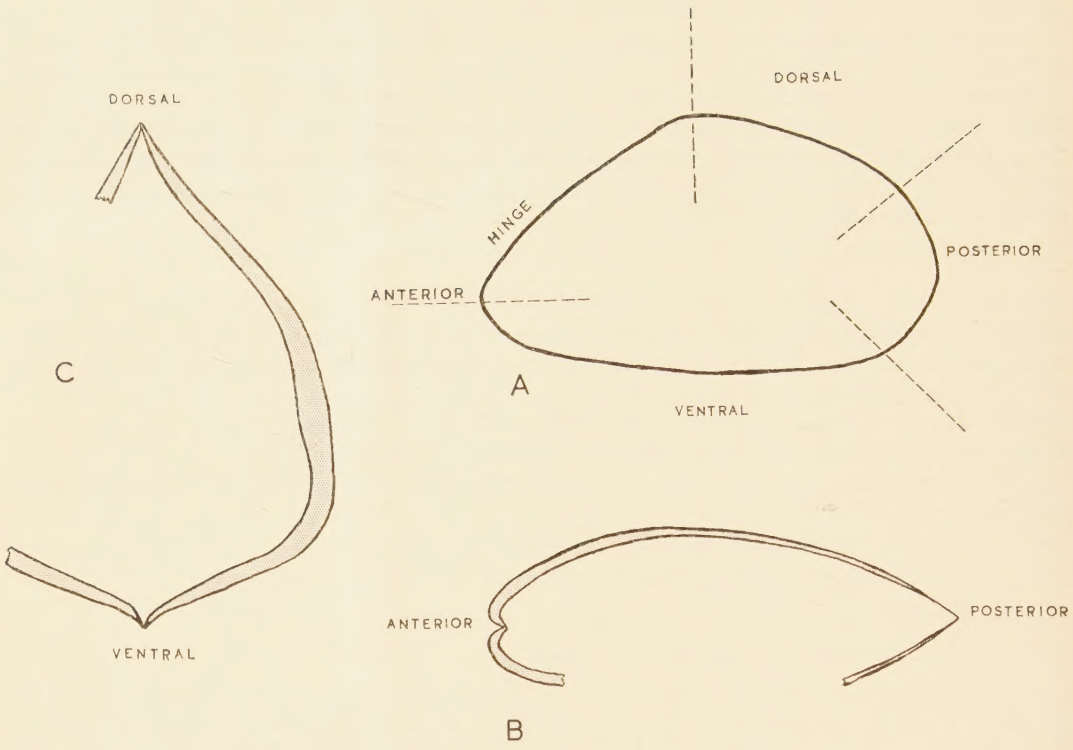


Fig. 1. *Shell morphology of the mussel* (*M. edulis*).
(*a*) The shell in profile with the terminology used in the text.
(*b*) A longitudinal section through the shell valves.
(*c*) A transverse section through the shell valves.

acute and the valves fit tightly: at the posterior margin the muscular adduction is least, especially ventrally, the shell thinnest, the angle between shell valves least, and the valves fit tightly: at the ventral margin, muscular adduction varies from a high value anteriorly to the lowest posteriorly, the shell is thick anteriorly but as thin posteriorly as the posterior margin, the angle between the shell valves is the largest for any region and the valves do not meet except by means of the thin periostracum.

The posterior and the posterior ventral margins would appear to be the most vulnerable, but in the case of attack by a series of blows from the bill, the relative importance of the factors contributing to vulnerability changes. In the majority of opened shells the strength of the shell and not its adduction appears to be limiting to vulnerability. Thickness, however, is not the decisive factor, since the largest shells found opened, over 60 mm., showed breakage ventrally in a relatively thick part of the shell. The acuteness of the angle between shell valves determines the size of the target their margins present. At the posterior margin the precision in direction of attack required to ensure more than a glancing blow is much greater than ventrally. On balance then, from mechanical considerations, the ventral margin is the most vulnerable to oystercatcher attack, especially posteriorly. This was confirmed by trials on live mussels in the laboratory. In respect of cockles (Drinnan, 1957) a similar conclusion was reached, the most vulnerable region being one where the valves did not meet and the angle between them was largest.

The orientation by the bird of the mussel with its most vulnerable ventral side uppermost—a relatively unstable position, which is maintained, the shell being re-orientated if it falls—points to a close adaptation of the feeding method to shell vulnerability. In contrast, when opening cockles, there was no restriction of effort to the most vulnerable place in the shell and the shell was placed in a relatively stable position. The direction of effort was to the valve margins generally rather than to any one region.

## FOOD INTAKE

The method of assessing food intake was that used earlier (Drinnan, 1957). Observations were made of mussels eaten by individual birds in a known time. With frequent counts of the percentage of birds feeding, an overall rate of food intake was obtained.

### MORFA

Timed feeding rate counts, 37 in all (Fig. 2A), were made on several visits to the beds between October 1955 and February 1956. On two occasions continuous observations were made over a full tidal cycle from High Water to High Water. Each count is based on a period of 5–10 min. Observation for a longer period would have been desirable, but was usually precluded by the weather.

As Fig. 2A shows, the feeding rate varied from 4 to 12 mussels per 5 min. but tended to be lower both at the beginning and the end of the feeding period, due, in all probability, to the small number of mussels exposed at these times. During the feeding period as a whole, feeding rate showed no correlation with tidal level on the beach, or substratum. Two

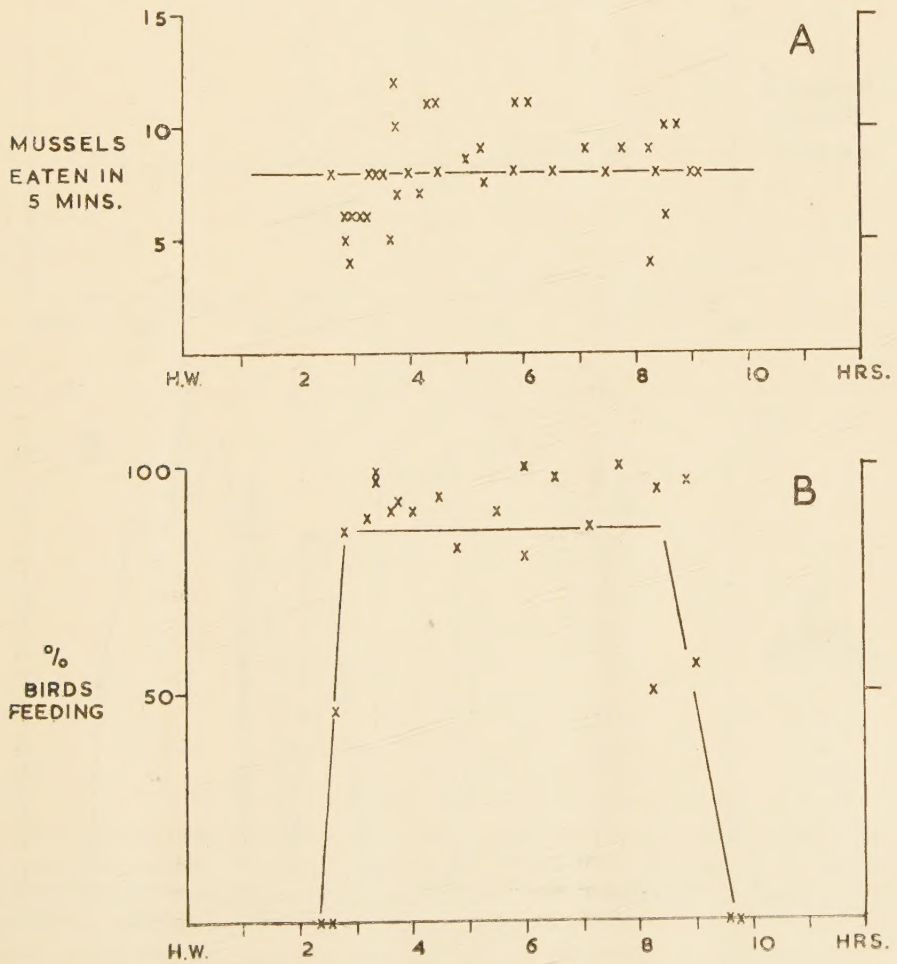


Fig. 2. *Details of oystercatcher feeding at Morfa.*

(*a*) Rate of eating mussels throughout the low tide feeding period. (H.W. = High Water. Broken line shows mean values.)
(*b*) as (*a*) Variation in percentage birds feeding.

birds which gave low figures stopped feeding while under observation and preened or bathed. It may well be that birds feed less actively as they approach satiation.

The results shown in Fig. 2A give an average feeding rate of 8·0 mussels per 5 minutes.

Percentage feeding counts were made whenever feeding was timed. The counts were usually based on a random sample of 100–200 birds but when the number of birds on the bed was already known, a count of those not feeding was made and the percentage feeding obtained.

The 20 counts made are shown in Fig. 2B. The birds fed for an average of 86% of a period from High Water + 2½ hours to H.W. + 9½ hours. The gradual build-up and fall-off in the number of birds feeding at the beginning and end of the feeding period was due to the birds' behaviour in forming and dispersing from the high water flocks, in small groups, the earliest birds preceding the last to arrive by about 30 minutes.

On combining the feeding rate counts with the percentage of birds feeding, we obtain an average overall feeding rate of 6·85 mussels/5 minutes or 82 mussels per hour for a total of 7 hours, a food intake for the tidal period of 574 mussels per bird.

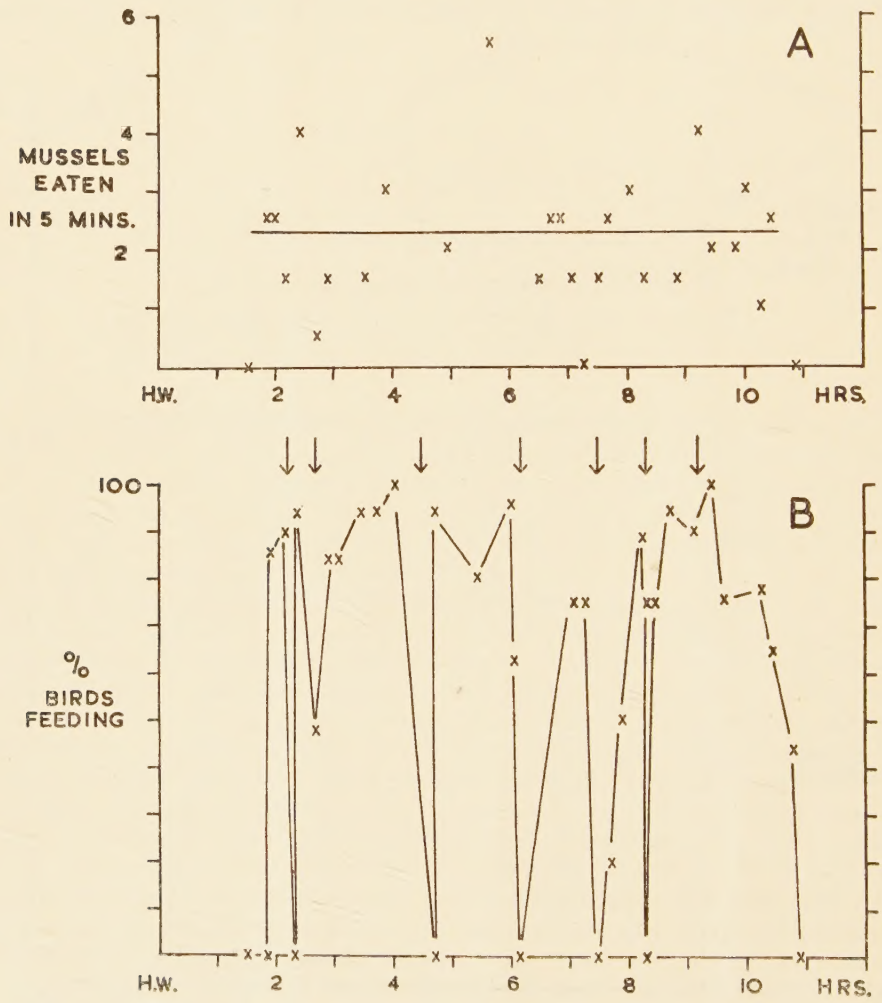


Fig. 3. *Details of oystercatcher feeding at Pensarn.*

(*a*) Rate of eating mussels throughout the low tide feeding period. (H.W. = High Water. The line shows mean value.)

(*b*) Variation in percentage birds feeding. The vertical arrows above the time scale mark times when human interference occurred.

PENSARN

Observations were made from the window of a laboratory on the foreshore. This enabled feeding rate counts to be based on periods of 10–20 min. but all such counts have been reduced to a basis of 5 minute periods for ease of comparison with the Morfa data. Counts of percentage birds feeding were made on the whole population, which is small.

Observations were made at frequent intervals throughout the winter 1955/56 but the data presented here (Fig. 3A), for reasons which will be clear later, are derived from observations made on 22 March 1956, covering a complete tidal cycle.

It can be seen that the observed feeding rates varied from 0·5 to 5·5 mussels per 5 minutes. This variation was due partly to the effect of human activities, which is dealt with more fully below, and partly to the size range of the mussels eaten. Table 1 shows the

Table 1: *Feeding rates of oystercatchers on mussels at Pensarn, Conway*

| *Feeding Rate* | *MUSSELS EATEN* | |
|---|---|---|
| *Mussels/10 mins.* | *Large* | *Small* |
| 3 | 1 | 2 |
| 3 | 2 | 1 |
| 3 | 1 | 2 |
| 3 | 1 | 2 |
| 3 | 1 | 2 |
| 4 | 1 | 3 |
| 4 | 0 | 4 |
| 5 | 1 | 4 |
| 5 | 0 | 5 |
| 5 | 2 | 3 |
| 5 | 2 | 3 |
| 5 | 0 | 5 |
| 6 | 2 | 4 |
| 6 | 0 | 6 |
| 6 | 0 | 6 |
| 8 | 1 | 7 |
| 8 | 0 | 8 |
| 11 | 0 | 11 |

details of feeding rate observations in 18 counts made when the effect of human interference was believed to be absent. In these counts eaten mussels were roughly classified into small (less than half the bill length) and large (more than half the bill length). It can be seen that the high counts comprise more small mussels than the low ones. This results from the greater time taken to open and eat a large mussel.

The average feeding rate from 26 observations is 2·3 mussels/5 minutes.

The counts of percentage of birds feeding made on 22 March are shown in Fig. 3B. The birds fed from H.W. + 2 hours to H.W. + 11 hours. This period is longer than that at the Morfa (H.W. + $2\frac{1}{2}$ to H.W. + $9\frac{1}{2}$); mussels occur at Pensarn at a higher level on

the beach at each end of the bridge, where the birds fed at the beginning and end of the feeding period.

Fig. 3B shows great variation in the percentage of birds feeding, at different times during the feeding period. This is a result of human activity which is a normal feature of this area and occurred as expected on the day of observation. In Fig. 3B the vertical arrows on the time scale mark times when human activity caused some or all of the birds to move to another feeding ground. The consequent drop in the percentage of birds feeding was usually very short-lived. Another effect of human activity, a drop in feeding activity often preceding actual flight, remarked on above, can be seen in Figs. 3A and 3B at H.W. − 2 hrs. 45 mins. and H.W. + 7 hrs. 15 mins. respectively.

By comparing the area covered by the 'percentage of birds feeding' curve to the area contained in the rectangle formed by H.W. + 2 hrs. to H.W. + 11 hrs. and the 100% level of feeding, we obtain an average of birds feeding of 75%.

Combining the feeding rates and percentage of birds feeding, we obtain an average overall feeding rate of 1·73 mussels per 5 min. or 20·75 mussels per hour for a total of 9 hours, an overall food intake for the tidal period of 186 mussels per bird.

## FOOD

No food other than mussels was seen to be taken by the oystercatchers observed in this study. Other oystercatchers fed regularly in other parts of the estuary, on sand and mud flats with no mussels present, and undoubtedly took other animals. These birds, however, formed a feeding flock quite distinct from the two described above.

Dewar (1915) states that 'each settlement (of oystercatchers) on the south shore of the Forth has an habitual range which it rarely exceeds. Individual settlements have not been known to trespass on each other's feeding grounds for the purpose of feeding.' In the Conway estuary also this is true. Three distinct flocks form; the two dealt with here, feeding on mussels at Morfa and Pensarn, and a third intermediate flock with a separate roosting ground and feeding grounds intermediate between Morfa and Pensarn. The first two areas are deserted in the summer, the third flock providing the summer population.

During periods of high water the birds which fed on the Morfa mussel beds formed a flock on dry barren sand and were never observed to feed. The mussel is therefore their principal, if not sole, food supply.

Many samples of opened shells were collected throughout the winter in both areas. In Figs. 4 and 5 the size distributions of these samples are compared with those of random samples of the populations. The population on which the Morfa birds were feeding (Fig. 4) comprises a single year class and the sample of 401 mussels shows a size-distribution between 12 and 27 mm. From this population the shells opened (Oct.-Jan.) ranged from 19 to 37 mm. Of this opened sample 25% exceed the largest size found in the population sample while mussels below 19 mm., which made up 41% of the population sample, are not represented at all. The birds select very strongly the largest mussels in the population, 25% of the opened mussels making up less than 0·2% of the population. These larger mussels were no longer to be found in the feeding area in March.

At Pensarn (Fig. 5) the size range of the population was much greater and the accuracy of the population sample probably much lower than at Morfa. The mussels opened by oystercatchers (18–61 mm.) cover much the same range as the general population (24–65 mm.). The smallest mussel opened (18 mm.) was very similar in size to that taken on the Morfa (19 mm.).

In earlier work on oystercatcher feeding (Drinnan, 1957) the food intake of the birds has been expressed as a meat volume in order to allow comparison with other areas and foods.

The volumes of the meats contained in the mussels in the two areas were measured by water displacement and the results are plotted in Fig. 6. From the samples of opened mussels the mean size of opened shells in the two areas are Morfa 25·7 and Pensarn 37·5 mm.;

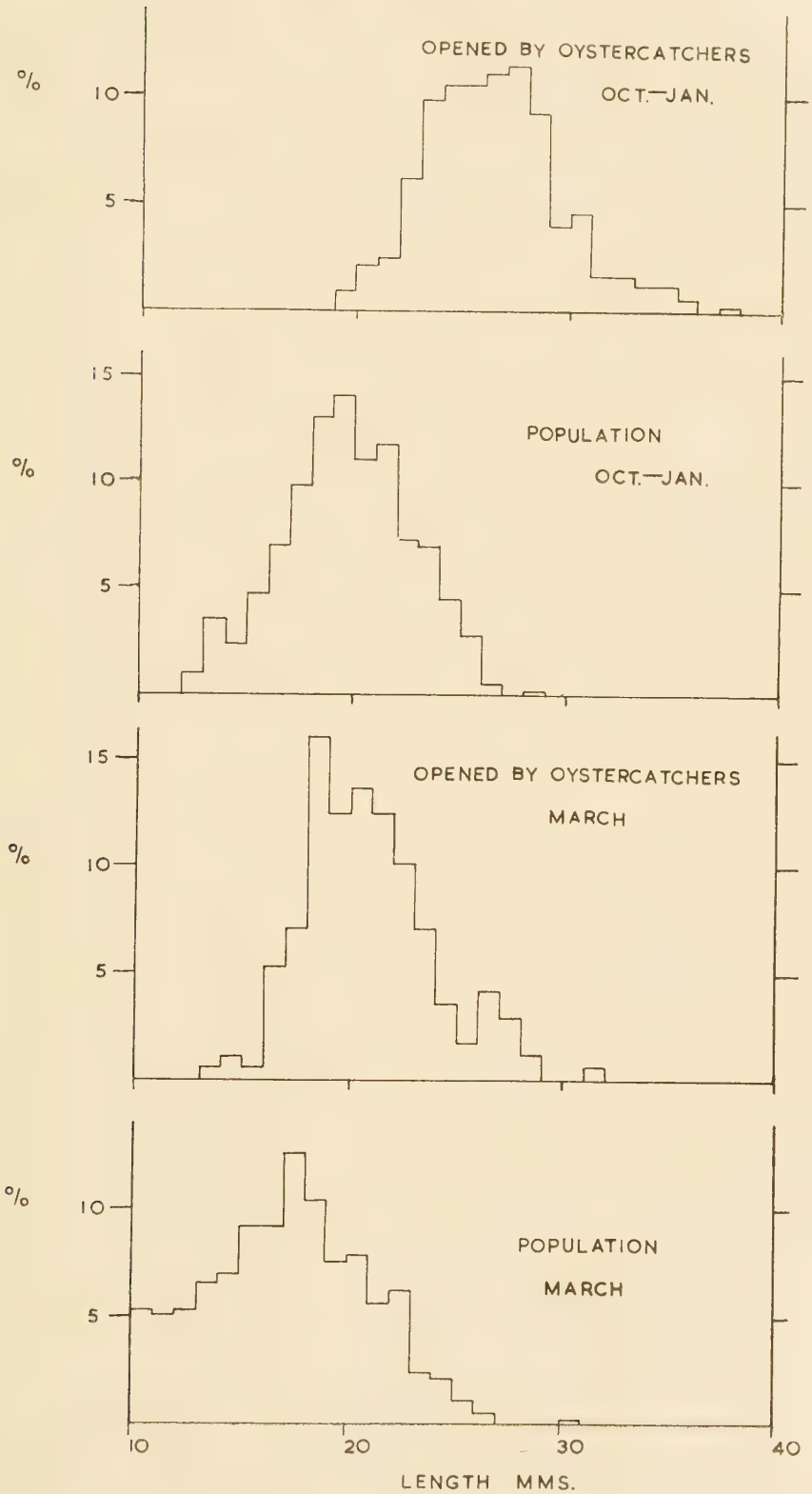


Fig. 4. *Size frequency distribution of mussels opened by oystercatchers at Morfa compared with that of the mussel population in October to January and March.*

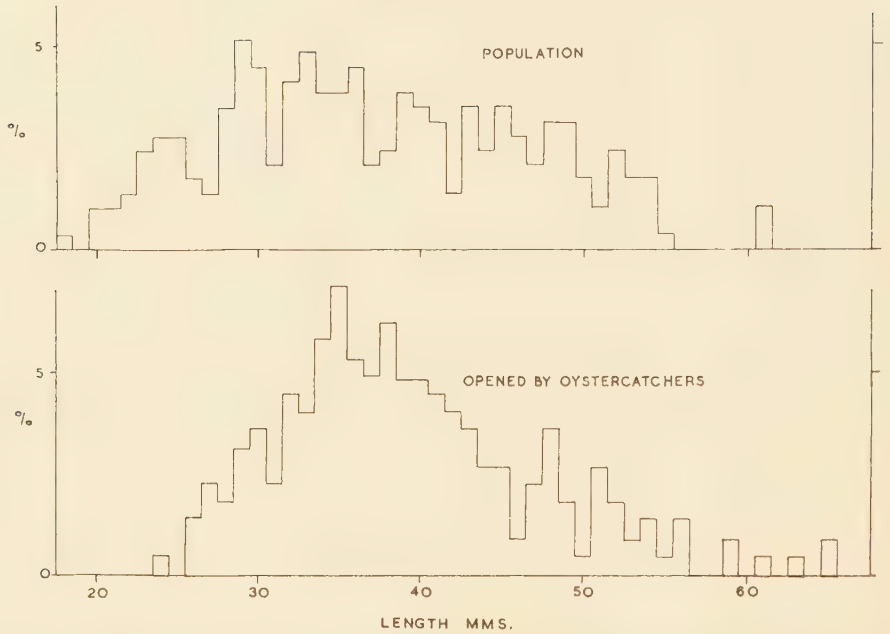


Fig. 5. *Size distribution of mussels opened by oystercatchers at Pensarn compared with that of the mussel population.*

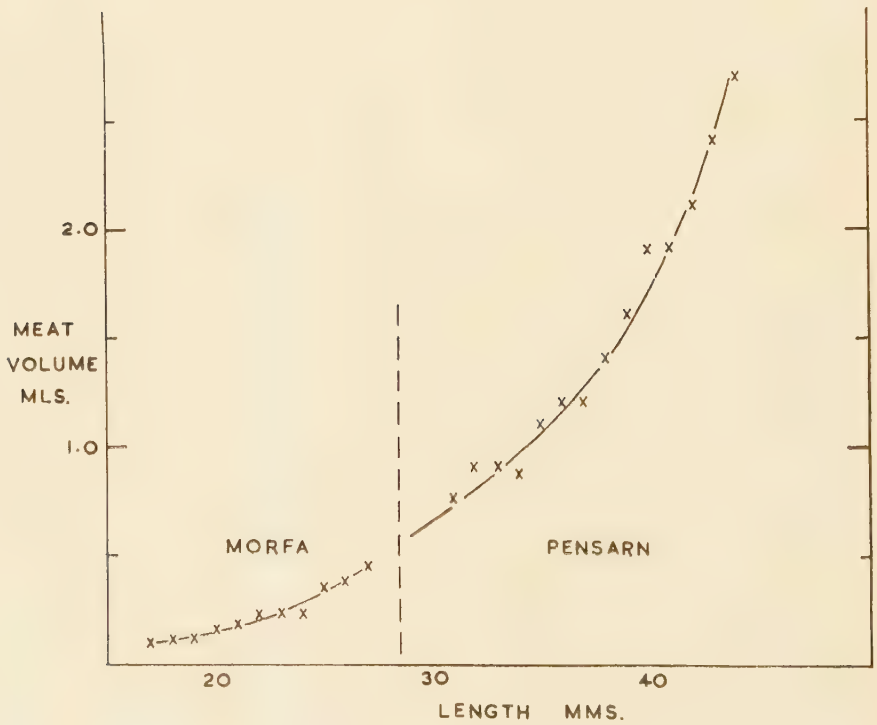


Fig. 6. *Volume of mussel meat/length of shell for Morfa and Pensarn.*

these give, from Fig. 6, volumes of 0·35 ml. and 1·35 ml. respectively.

From the overall food intakes calculated above, we obtain the following meat volumes:

Morfa. 574 mussels with mean meat volume 0·35 ml. = 200·9 ml. meat per tidal cycle.

Pensarn. 186 mussels with mean meat volume 1·35 ml. = 251·1 ml. per tidal cycle.

Estimates from other areas are very similar, with a mean figure of 200 ml. per tide. This gives (Drinnan, 1957) a food intake (dry weight) of 20% of the bird's own weight per day. Expressed in another way, each bird eats a wet weight of shellfish flesh per day roughly equivalent to its own weight.

## BIRD NUMBERS

During the survey, periodic counts were made of the numbers of birds in the two flocks. The flock at Pensarn was counted by eye at frequent intervals between September 1955 and March 1956, and varied from 18–25 birds. The Morfa flock was estimated by eye at frequent intervals and also counted by a photographic method (Drinnan and Ridpath, 1957) on a few occasions in the spring of 1956. The flock was first seen on 30 July 1955 when an estimated 700 birds flew down the river to the Morfa mussel beds. This flock remained approximately constant in numbers until February 1956. Photographic estimates of 729 and 779 birds were made on 4 and 5 January. From the end of January, a gradual decline in numbers was seen, and a photographic estimate of 588 birds was made on 25 February and another of 344 birds on 15 March. By the end of March the total had dropped to the summer population level of under 50 birds.

## PREDATION

The present work presents the basic biological knowledge required to assess the importance of oystercatcher predation in a mussel-bearing area with the minimum additional local observations such as bird numbers and mussel population parameters. With the vast population of the Conway mussel beds and the relatively few oystercatchers present the effect of predation would appear to be small, although local effects may be considerable.

The opened mussel samples from Morfa used in this paper were collected between October 1955 and February 1956, when most of the observations were made. Late in March another sample was taken and compared with these, the mussel population being sampled at the same time. All the samples were taken from the same small area where oystercatchers fed all winter.

The size distributions of the four samples are shown in Fig. 4. There is an obvious difference in the size distributions of the opened mussels. The mussels above 28 mm. in length, for which the oystercatchers showed a high degree of selection in October-January, are not present in the March sample, the size distribution of opened mussels more nearly approaching that of the population. The two samples of the population show little difference beyond a slight decline in the proportion of the larger size groups. In both these samples, mussels below 10 mm. in length were discarded. The increase in the proportion of the smaller size groups in the March population sample is probably due in part to growth.

The indication from the graphs that the larger size groups which were eaten preferentially in October-February were not present in March, was confirmed by the examination of several thousand mussels. Mussels above 28 mm. in length were virtually absent from the population, though in January when this size range was needed for the measurement of meat volumes specimens were easily found. It is suggested that the oystercatchers had virtually eaten out the larger size groups by late March.

Dewar (1915) describes samples of opened mussels collected over the winter 1908/1909. Though his samples are small, he claims a decrease in average size of these mussels. Similar samples of other food organisms, *Modiolus*, *Tapes* and *Patella* showed the same trend.

# DISCUSSION

THE results described above differ considerably from those obtained by Dewar (1908, 1913, 1915) from the Firth of Forth, but most of the divergences can be related to a difference in feeding behaviour.

Dewar states (1915) that 'the oystercatcher cannot open a mussel when it is tightly closed, unless the byssal cleft can be reached, or the mussel is small enough to be crushed.' Although he described the carrying of mussels before opening, the majority of opened mussels examined had been dealt with *in situ*. In the position occupied by many mussels, with the ventral surface on the substrate, only the dorsal and posterior margins of the valves are approachable. As mentioned above, the oystercatchers under observation in the present study seldom opened a mussel *in situ;* after being detached from the substrate, they were usually placed with the ventral margin of the valves uppermost and attacked in this region. There was no indication that mussels which had been exposed to the air for some hours presented any greater problem in opening than newly exposed or submerged mussels.

This difference in feeding behaviour is reflected in the damage to the shell. Dewar quotes 78% opened through the dorsal border, 13% through the posterior border, and only 9% through the ventral border. These are to be compared with 1% opened through the dorsal border, 3–4% through the posterior and 75–83% through the ventral, from above, the balance being made up by undamaged shells, probably opened through the ventral border. Confirmation of the suggestion that a different feeding habit is responsible for this difference is available from Dewar's (1913) observations on the opening of *Modiolus modiolus*. The method of opening was the same as observed for *Mytilus* in the present study. 'The shells are entered and opened up precisely as if they were those of the edible mussel. But in the majority of cases they are dragged from their anchorage before being levered widely open and cleaned of their contents'. The recorded damage to shells shows, over a size range of 19 to 57 mm., 30% opened through the dorsal border, 6% through the posterior border and 64% through the ventral border. As Dewar notes 'these figures roughly reverse the percentages obtained from *Mytilus edulis*', and more nearly approach the figures obtained for *Mytilus* in the present work.

Dewar in speaking of feeding behaviour says 'As the scalps become dry the birds turn their attentions to the edges of the banks, the adjacent sand or mud and the pools in quest of hidden mussels. The period of slack water is devoted to repose . . .' In the present work no such low water cessation of feeding was seen. A possible parallel to this situation may be the differences observed between the behaviour of oystercatchers feeding on cockles in Morecambe Bay and at Brancaster Harbour (Drinnan, 1957). In these two areas the food intake was much the same but whereas in Morecambe Bay feeding continued throughout the low tide period, at Brancaster the birds fed only for a period on the ebb and flood, at a higher rate than at Morecambe Bay, and rested at low water. Dewar makes little mention of feeding rates but an isolated observation (Dewar, 1913) of over 400 mussels 20 mm. in length taken in one hour by a single bird, suggests that feeding rates were high.

Dewar came to the conclusion that 'oystercatchers show a decided preference for mussels about 3·5 cm. in length'. This was not confirmed. Though at Morfa the birds selected very vigorously mussels of this size, from a population of which they were the largest (Fig. 4), at Pensarn no preference for this size of mussel was shown (Fig. 5). Possibly the preference observed by Dewar was a result of opening *in situ* where the difficulty in opening a mussel probably increases greatly with size, if the byssal cleft cannot be utilised. The largest opened mussel seen by Dewar (1913) was 50 mm. in length, and this had been detached and opened through the byssal cleft, whereas opened mussels of over 60 mm. were not uncommon at Conway (Fig. 5).

Dewar (1915) studying the effect of human activities found that 'the situation of the feeding ground at or more than 150 metres from the nearest danger point is also an adjustment, probably local, to human intervention'. In the Conway estuary at both Pensarn and Morfa the birds would show no reaction until approached within 50 metres. It has been noted that in all areas in which oystercatchers have been studied, reaction to human intrusion decreases throughout the winter.

## SUMMARY

OBSERVATIONS were made on the feeding of the oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*) in the estuary of the River Conway, Caernarvonshire, in the winter 1955–56.

Feeding was studied on the mussel beds at the river mouth (Morfa) and in an area higher up the estuary above the suspension bridge (Pensarn). The oystercatcher populations of these areas are discrete.

The birds are present between August and late March and are probably British breeding birds.

Feeding follows the tidal cycle, continuing throughout the period when mussels are uncovered, high water periods being spent in non-feeding roosting flocks. This cycle continues during darkness.

The feeding behaviour of the birds is described for the two areas. The method of gaining entry to the shellfish is related to the observed damage to the opened shells.

Quantitative data on food intake for the daylight feeding period are given. Figures obtained are Morfa 574 mussels (average length 25·7 mm.)/low tide period/bird, and Pensarn 186 mussels (average length 37·5 mm.)/low tide period/bird. Expressed as volumes of wet meat, these figures are equivalent to 200 ml. and 251 ml. respectively for Morfa and Pensarn. Each bird eats about its own weight of wet shellfish per day.

No precise measure of the effect of oystercatcher predation on the mussel population was made, but, at the Morfa, population samples through the winter showed the steady removal of the larger size groups by the birds.

The present work is compared with the results obtained by Dewar and the many divergences noted. These can all be ascribed to differences in feeding behaviour of the birds in the two studies.



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